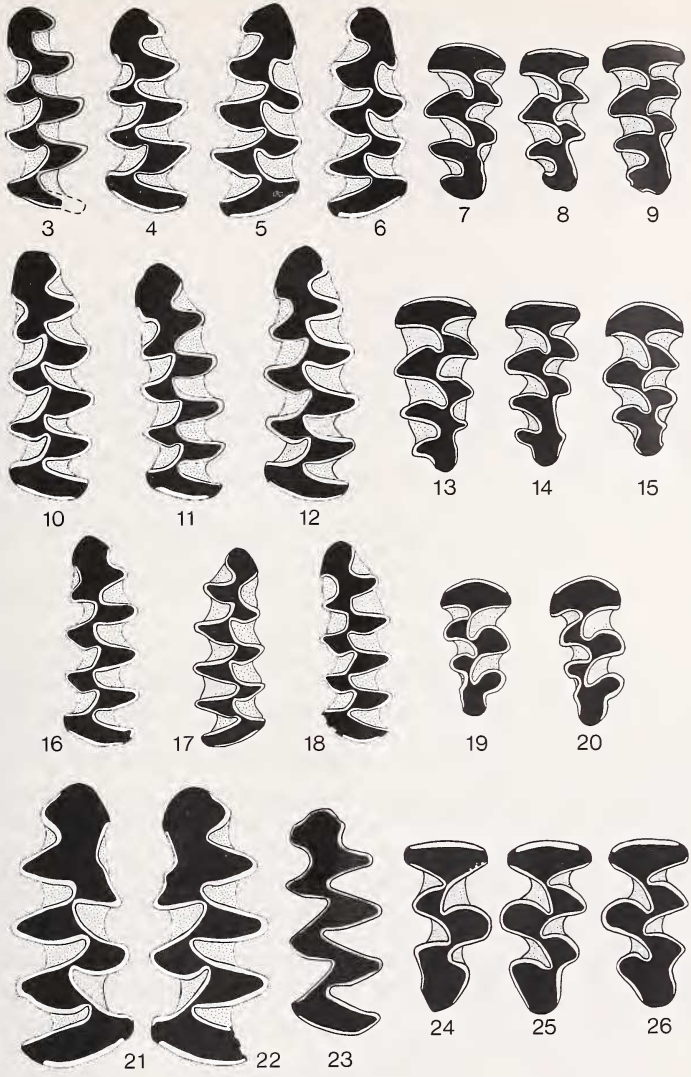

Abb. 3. Arvicolidenzähne von Karain B in Occlusalansicht. *Microtus gud:* 3–6 = M/1, 7–9 = M3/; *Microtus guentheri:* 10–12 = M/1, 13–15 = M3/; *Microtus arvalis:* 16–18 = M/1, 19–20 = M3/; *Arvicola* sp.: 21–23 = M/1, 24–26 = M3/

zän von Chios (Storch 1975). Der Artname wird zunächst offengelassen, bis besser erhaltenes Material die Überprüfung auch anderer Merkmale erlaubt.

Zahnmaße von *Arvicola* sp. aus Karain: M/1 = 3.1–3.8, M3/ = 2.3–2.4 mm.

Danksagungen

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Zusammenfassung

Ausgehend von günstigeren Umweltverhältnissen im Mittelpaläolithikum nahmen im Älteren Jungpaläolithikum Aridität und Offenland zu. Bei fortbestehender Dominanz von Steppenverhältnissen zeichnen sich im „Epipaläolithikum" kürzere klima-ökologische Oszillationen ab. *Microtus gud* wurde offenbar gebietsweise durch den weniger hygrophilen *M. nivalis* als spätem Immigranten von Westen her ersetzt. *Mus abbotti* erscheint gegen Ende der pleistozänen, *Meriones tristrami* erst mit holozänen Schichtenfolgen. Einige Arten verschwinden im Jungpleistozän für immer aus dem Gebiet; trotzdem ist eine bedeutende ökologische und faunistische Stabilität zu erkennen.

Literatur

Albrecht, G. (1986): Die Höhlenstation Karain bei Antalya/Türkei. Sondage durch das Institut für Urgeschichte der Universität Tübingen im Herbst 1985. Mittbl. Archaeol. Venatoria **10/11**, 22–36.

Besenecker, H.; Spitzenberger, F.; Storch, G. (1972): Eine holozäne Kleinsäuger-Fauna von der Insel Chios, Ägäis (Mammalia: Insectivora, Rodentia). Senckenbergiana biol. **53**, 145–177.

Corbet, G. B.; Morris, P. A. (1967): A collection of recent and subfossil mammals from southern Turkey (Asia Minor), including the dormouse *Myomimus personatus*. J. nat. Hist. **4**, 561–569.

Felten, H.; Spitzenberger, F.; Storch, G. (1971): Zur Kleinsäugerfauna West-Anatoliens. Teil I. Senckenbergiana biol. **52**, 393–424.

Kratochvíl, J. (1986): *Mus abbotti* – eine kleinasiatisch-balkanische Art (Muridae – Mammalia). Folia Zool. **35**, 3–20.

Kumerloeve, H. (1975): Die Säugetiere (Mammalia) der Türkei. Die Säugetiere (Mammalia) Syriens und des Libanons. Veröff. zool. Staatssamml. München **18**, 69–225.

Kuss, S. E.; Storch, G. (1978): Eine Säugetierfauna (Mammalia: Artiodactyla, Rodentia) des älteren Pleistozäns von der Insel Kalymnos (Dodekanés, Griechenland). N. Jb. Geol. Paläont. Mh. **1978**, 206–227.

Orsini, Ph.; Bonhomme, F.; Britton-Davidian, J.; Croset, H.; Gerasimov, S.; Thaler, L. (1983): Le complexe d'espèces du genre *Mus* en Europe Centrale et Orientale. II. Critéres d'identification, répartition et caractéristiques écologiques. Z. Säugetierkunde **48**, 86–95.

Osborn, D. J. (1962): Rodents of the subfamily Microtinae from Turkey. J. Mammalogy **43**, 515–529.

— (1965): Rodents of the subfamilies Murinae, Gerbillinae, and Cricetinae from Turkey. J. Egyptian publ. Health Assoc. **40**, 401–424.

Röttger, U. (1986): Schmelzbandbreiten an Molaren der Gattung *Arvicola* Lacépède, 1799. Unveröffentl. Inaugural-Diss. Med. Fakultät der Rheinischen-Friedrich-Wilhelms-Universität Bonn, 1–121.

Spitzenberger, F. (1971): Zur Systematik und Tiergeographie von *Microtus (Chionomys) nivalis* und *Microtus (Chionomys) gud* (Microtinae, Mamm.) in S-Anatolien. Z. Säugetierkunde **36**, 370–380.

— (1972): Der Hamster *Mesocricetus brandti* (Nehring, 1898) in Zentralanatolien. Z. Säugetierkunde **37**, 229–231.

Steiner, H. M. (1972): Systematik und Ökologie von Wühlmäusen (Microtinae, Mammalia) der vorderasiatischen Gebirge Ostpontus, Talysch und Elburs. Sitzungsber. österr. Akad. Wiss., math.-naturwiss. Kl., Abt. I **180**, 99–193.

Storch, G. (1975): Eine mittelpleistozäne Nager-Fauna von der Insel Chios, Ägäis (Mammalia: Rodentia). Senckenbergiana biol. **56**, 165–189.

— (1977): Die Ausbreitung der Felsenmaus *(Apodemus mystacinus):* Zur Problematik der Inselbesiedlung und Tiergeographie in der Ägäis. Natur u. Museum **107**, 174–182.

— (1978): Familie Gliridae. In: Handbuch der Säugetiere Europas. Hrsg. J. Niethammer; F. Krapp. Wiesbaden: Akademische Verlagsges. Bd. 1/I, 201–280.

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Vocalizations of captive Water mongooses, *Atilax paludinosus*

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Abstract

The vocalisations of water mongooses were recorded and analysed sonagraphically. Three main types of sounds were recognised, namely "bray types", "grizzle types" and "humph types". "Bray types" were produced during mating and also in some agonistic encounters. "Grizzle types" were produced by both old and young animals and indicated either distress or a warning. "Humph types" were the only sounds that were characterised by some frequency modulation and were interpreted as either attention or appeasement calls. Compound calls were also recorded and consisted of two or more of the above types produced in rapid succession. It is suggested that the few sounds made by *Atilax* represent the basic pattern from which the more complex vocal patterns of sociable herpestines have developed. This suggestion does not, however, assume that the calls of *Atilax* are primitive, as they are well adapted to the mongooses way of life.

Introduction

The variety of vocalisations produced by water mongooses is limited, unlike those of the Indian mongoose *Herpestes auropunctatus* (Mulligan and Nellis 1975), the dwarf mongoose, *Helogale undulata rufula* (Maier et al. 1983) the banded mongoose, *Mungos mungo* (Garratt 1978) and the suricate *Suricata suricatta* (Ewer 1973). Water mongooses are solitary and nocturnal or crepuscular herpestines. Although relatively silent on their own, the variety of calls produced during social interactions indicates their ability to communicate adequately when necessary. However, the limited vocal repertoire of *Atilax*, when compared with the extensive and complex repertoire of sociable herpestines (Ewer 1973; Garratt 1978), indicates that sociable mammals develop a wider vocabulary in response to the demands of group living. In addition to vocalizations, water mongooses communicate behaviourally through facial expression and body posture as well as through chemical means. Both behavioural and chemical communication will be presented elsewhere.

Material and methods

The data presented here were obtained from eight captive water mongooses which were housed either singly or in pairs in outdoor enclosures measuring 1,5 × 3 × 1,2 m. Details regarding their maintenance are given in Baker (1987) and Baker and Meester (1986). Recordings were made on an Uher 4000 Report-L tape recorder at a speed of 9,5 cm using either an Uher M517 microphone or a D.K.G. model D58E directional microphone. Acoustic analysis was performed using a Kay Sonagraph 7029A. For most of the recordings a frequency range of 80 to 8000 Hz was selected, although 40 to 4000 Hz was used for sounds of low frequency. In all cases the narrow filter bandwidth of 45 Hz was selected.

Although attempts were made to eliminate background noise during recording sessions, many sonagrams show low frequency noise.

The parameters that were described for each sonagram are defined as follows (Eisenberg et al. 1973; Rossing 1982):

1. Fundamental frequency: The component of a sound of the lowest frequency;
2. Harmonics: The components of a sound whose frequencies are multiples of the frequency of the fundamental frequency;
3. Duration: Time of each call or its components (syllables);

4. Syllable: Basic call element that manifests itself as an uninterrupted tracing on the horizontal axis of the sonagram;
5. Phrase: Group of syllables separated from other syllables by a time interval greater than any time interval separating the syllables in a phrase;
6. Tonal syllable: Harmonic syllable;
7. Noisy syllable: Sound not organised into discrete energy bands;
8. Mixed syllable: Appears on a sonagram as a superimposition of noise upon a harmonic series;
9. Long syllable: More than 0,6 seconds in duration;
10. Short syllable: Exceeds 0,05 seconds and less than 0,6 seconds in duration;
11. Formant: A range of frequency to which a system responds preferentially or which is emphasised in its output.

The context in which the sounds were made was recorded and briefly described.

Results

One hundred and forty-three sounds were sonagraphed and classified into three main types (Fig. 1). Each type was further divided into different forms showing basic similarities. Type one, called "bray types", consists of long or short mixed syllables which

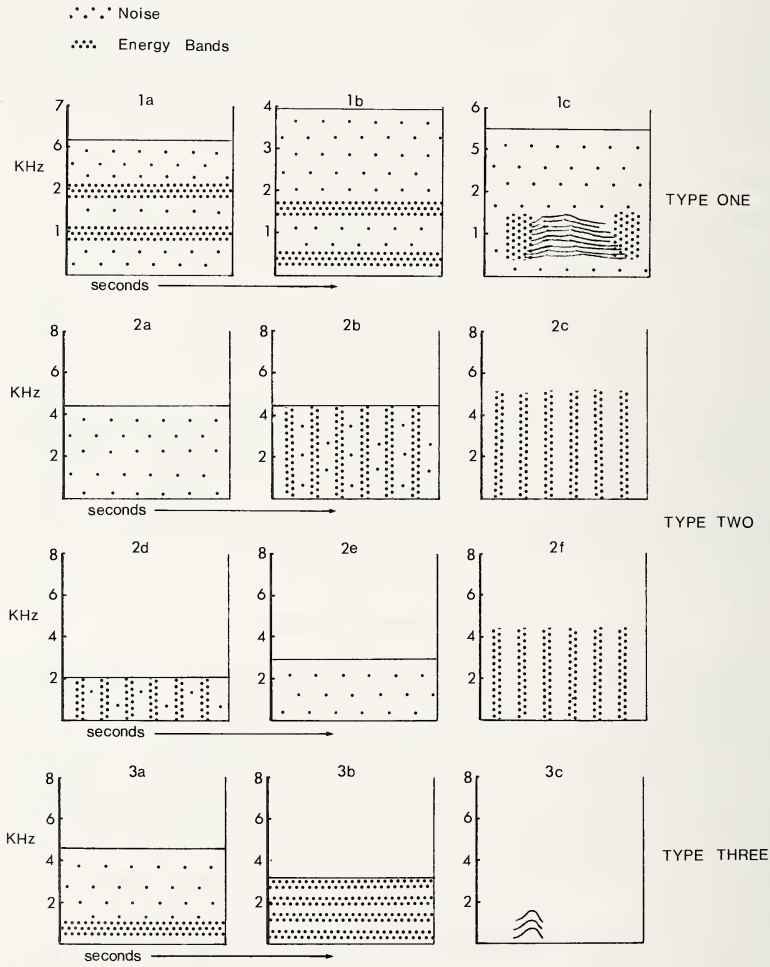

Fig. 1. Three main types of calls produced by *Atilax paludinosus*

Table 1. **Variation in Type 1 calls**

	Type 1a		Type 1b		Type 1c		ANOVA		
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	F	P	S
Duration	0.65	0.26	0.99	0.79	0.86	0.86	0.79	0.48	NS
Fundamental frequency	1	–	0.58	0.26	0.5	–	9.63	0.007	S
Harmonic number	1	–	1	–	14	–	–	–	–
Maximum frequency	6.29	1.79	3.93	0.51	5.5	–	3.65	7.25	NS

exhibit pronounced bands of energy. Type two, called "grizzle types", are characterised by the presence of pulses. The calls vary in amplitude, and may be long or short and noisy or mixed. Type three, called "humph types" are short, with tonal or mixed syllables. Some frequency modulation is usually apparent.

Type one: The three different forms of this call (n = 12) are produced mainly in the context of mating (75 %) and also in some agonistic encounters (25 %). During a mating sequence it is always the female that produces the sound during the initial chase and avoidance phase when she attempts to escape the male. In aggressive encounters it is always the subordinate that calls. The posture of this animal is characteristically submissive with the shoulders at a lower height than the haunches, and often the head is tilted upwards or backwards, pointing towards the dominant animal. The mouth is usually wide open.

Forms 1a and 1b (Fig. 2) are very similar (Table 1) but are significantly different with

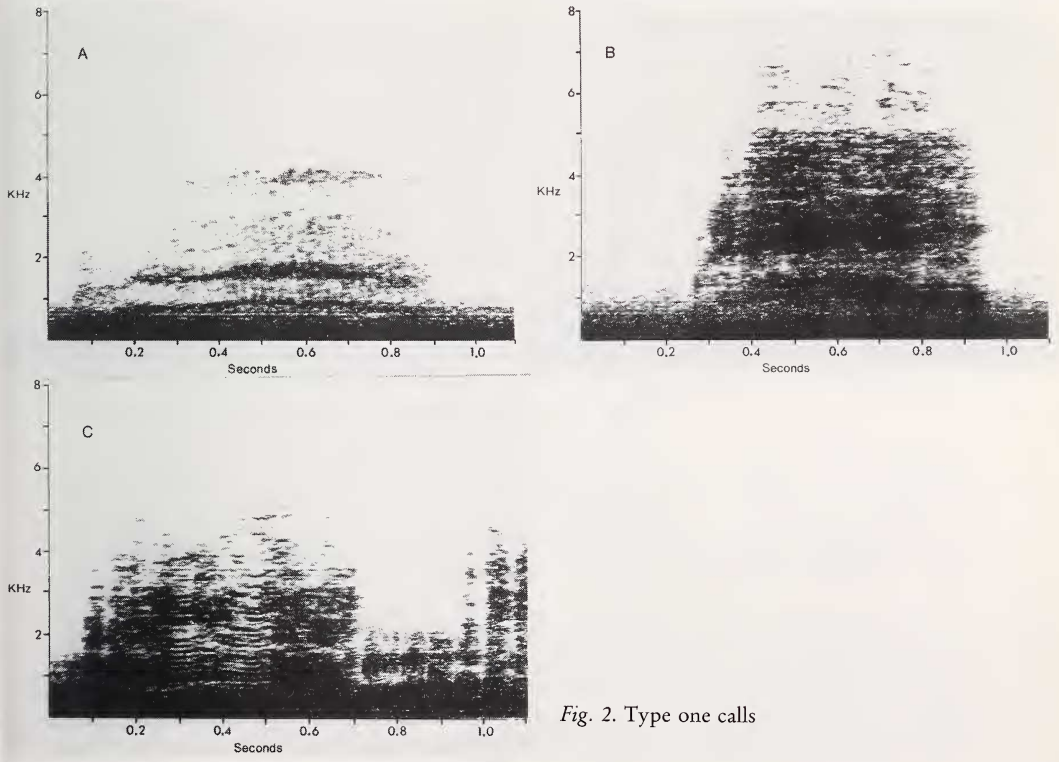

Fig. 2. Type one calls

Table 2. **Variations in Type 2 calls**

	Type 2a		Type 2b		Type 2c		Type 2d		Type 2e		Type 2f		ANOVA	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	F	P	Signif.
Duration	0.98	0.46	0.85	0.6	0.31	0.31	1.37	1.47	1.14	0.87	0.97	0.73	2.65	0.02	S
Maximum freq.	4.54	1.04	4.5	0.97	5.12	1.60	2.00	0.93	3.08	0.64	4.58	2.20	0.69	0.62	NS
Formant	1.61	0.56	1.79	0.67	1.81	0.37	0.66	0.14	0.89	0.3	1	–	9.62	0.000001	S
No. of pulses	–	–	9.03	7.6	4.25	0.5	24.3	20.03	–	–	7.66	3.88	6.52	0.0008	S

respect to their fundamental frequencies (t = 3,92; p = 0,004; df = 8) and maximum frequency (t = 2,51; p = 0,036; df = 8). Form 1c (Fig. 2) is clearly different from 1a and 1b due to the presence of more than one harmonic. However, there are marked similarities in duration, maximum frequency and fundamental frequency (Table 1). Form 1c was produced exclusively prior to mating.

All three of these forms may be repeated within 0,6 seconds, usually depending on the intensity of interaction between two mongooses.

Type two: Table 2 shows the main parameters of these forms (n = 94). There are clearly two groups, one of a higher frequency (2a, 2b, 2c) than the other (2d, 2e, 2f) (Fig. 3). The sounds are made equally by both adults and juveniles, although 2c is exclusively an adult sound.

In most instances (52,1 %) these calls indicated distress, resulting from frustration of goal-directed behaviour. In social encounters they are most commonly produced by a submissive animal during agonistic displays (40,4 % of the time). Grizzles are the sounds most commonly found in captive handraised animals, probably resulting from their restriction. Wild, captive mongooses produce these "grizzle" sounds (2a, 2b, 2f and 2e) (Fig. 3) only in the context of agonistic encounters or in parent-young interactions. In agonistic encounters they often precede a confrontation and are produced by the submissive animal. In parent-young interactions the sound may be made by the mother when she is avoiding her offspring, in which case it serves as a warning, or when she is engaged in play-fighting. During these sequences it is the young that call as they are clearly subordinate to the mother. The young "grizzle" when left alone by the mother indicating that they are disgruntled; when playing roughly with each other or their mother as a form of protest; and also when unwilling to be groomed by the parent. In the last two situations the call signals a need to be released.

Form 2e (Fig. 3) is primarily produced by very young animals (96,4 % of the time, n = 28) and never exhibits pulses. It is a low frequency, noisy sound which may have a formant at 0,89 Hz on average (n = 28, SD = 0,3). It is mostly used when the parent leaves the nest for foraging or when the young have managed to emerge from the nest and are clearly disorientated.

Form 2d (Fig. 3) is a growl which is distinct from the others in always being of low frequency, and varying widely in duration (Table 2). The pulse frequency is remarkably constant at 0,025 seconds. Of the 14 incidences of growling 14,2 % were made during mating sequences, 50 % were feeding growls and the remainder (35,8 %) were threats made by adults towards the observer.

Form 2c (Fig. 3) is a cackle produced by adults. It is a

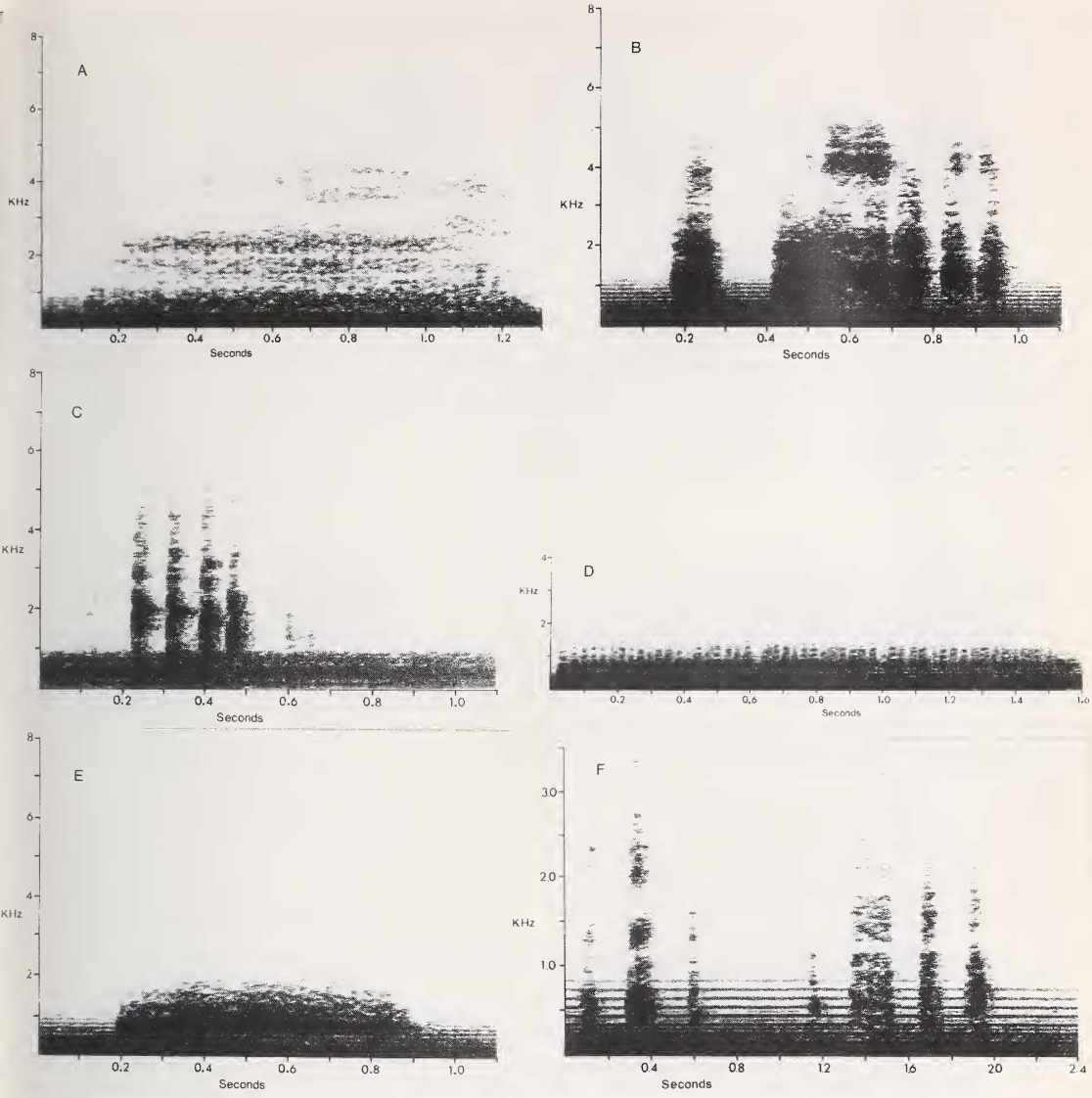

Fig. 3. Type two calls

loud explosive, clear and concise sound. The growl and the cackle are produced as a threat or when surprised.

The pulse interval in type two calls varies from 0,025 seconds to 0,28 seconds, $\bar{x}$ = 0,07 seconds, SD = 0,04.

Type three: The main parameters of type three calls n = 37 are presented in Table 3.

Both young and older animals produce these calls, although 3c is exclusively produced by very young mongooses when calling for attention. Forms 3a and 3b (Fig. 4) were also made to attract the attention of the parents. In older animals 3a and 3b were often produced in anticipation of food. During mating sequences the male was heard calling

Table 3. **Variations in Type 3 calls**

	Type 3a		Type 3b		Type 3c		ANOVA		
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	F	P	Signif.
Duration	0.28	0.04	0.32	0.13	0.28	0.06	0.99	0.37	NS
Maximum frequency	4.58	1.49	3.26	1.03	1.75	0.28	11.56	0.0001	S
Fundamental frequency	–	–	0.56	0.11	0.51	0.04	0.84	0.37	NS
Harmonic No.	–	–	5.87	2.58	2	0.03	12.64	0.003	S
Max. freq. modulation	–	–	–	–	0.35	6.64	–	–	–

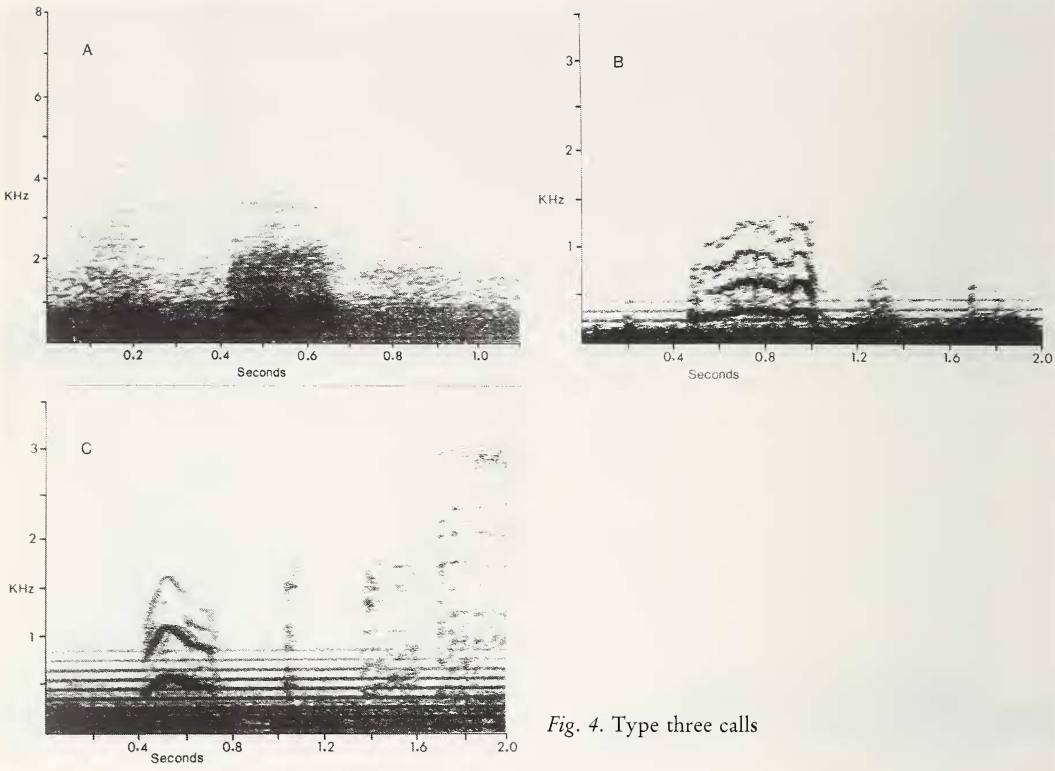

Fig. 4. Type three calls

when confronted with an unwilling female. Because this sound was made only in response to a female threatening a persistent mate (in the context of mating) during the initial phases of the mating sequence, it indicates an appeasement function.

Form 3c exhibits a marked frequency modulation (Fig. 4; Table 3), and is the only water mongoose call to do so.

Occasionally different sounds were grouped together to form a compound call. Most commonly "grizzle" sounds were repeated to form a phrase, although some sounds consisted of a series of the above types following one another sequentially, or superimposed one upon the other (Fig. 5). Most commonly there was a combination of types two and three, beginning with a "grizzle" and ending with a "humph". Type two ("grizzle") might also be followed by a type one sound ("bray").

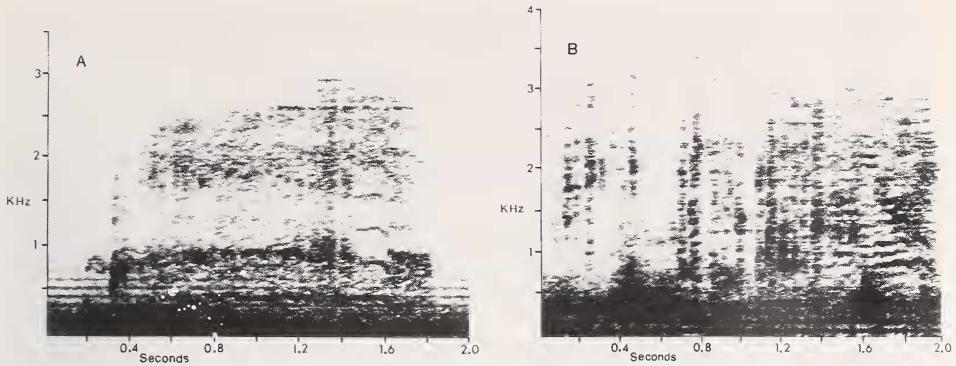

Fig. 5. Compound calls produced by *Atilax*. A: Grizzle followed by humph; B: Grizzle followed by bray

Discussion

Although the variety of vocal sounds made by captive *Atilax* is poor, their inherent variability is extensive, especially when duration and maximum frequency are considered.

The only other major variant is the number of pulses that occurs in Type 2 calls. This is clearly related to duration, as the longer the calls the greater the number of pulses. The variation in pulse intervals shows no clear pattern, and is neither sex- nor age-related, as both young and old animals exhibit both extremes of the range.

Eisenberg et al. (1973) discuss variability within the categories of sounds produced by marsupials, and note that a number of transitional forms of the defined type may exist, such that the distinctness of two types becomes confused. Further, the sounds that are used as the categorical type are usually at the extremes of a graded series of sounds, and thus are quite distinct. In *Atilax* there are some sounds that may structurally appear to fit into one category or another, such as types 1a, 2a and 3a sounds. It is often only the auditory perception of the sound in conjunction with its visual context that provides the key to the category in which it belongs.

The variation in *Atilax* calls may have one or more of several determinants, most notably individual variation or age-related differences. In addition, a solitary mongoose with its limited vocal repertoire demands less specificity with respect to the sounds that it makes, as there is little chance of confusion when so few calls make up the entire vocabulary. In a social animal with a wider range of different calls it becomes important to ensure correct understanding of specific signals, as these are crucial in maintaining group understanding. Therefore it would be expected that greater attention would be paid to pronouncing the sounds concisely.

The tendency in colonial birds (Wiley 1976) is towards reduction in the variety and detail of calls as these become confused in the noisy environment of a breeding colony. This may be an important factor influencing the vocalisations of mammals, and would be most clearly illustrated amongst some of the sociable herpestines. However, the available information on vocal repertoires of sociable mongooses indicates a deviation from this pattern, which may also be representative of other mammalian groups.

When compared with vocalisations of *Mungos mungo* (Garratt 1978) and *Herpestes auropunctatus* (Mulligan and Nellis 1975) it becomes clear that the sounds made by *Atilax* are a basic type that is found within the repertoire of these other two species, and which has in some instances been slightly modified (e.g. the weeonk call of *Herpestes*